ABSORPTION OF MANGANESE BY PLANTS. II.

TOXICITY OF MANGANESE TO VARIOUS PLANT SPECIES

BY

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Introduction.

In 1934 the writer (20) published some studies which show, for one thing, that plants absorb increasing quantities of manganese with increasing hydrogen ion concentration of the soil. Plants which grow in neutral or basic soil thus contain as a rule only a few mg. manganese per 100 g. dry leaf material, while plants which grow in strongly acid soil may contain over 200 mg. manganese per 100 g. dry leaf material.

In the same paper the writer also describes a water culture experiment which showed that even a concentration of 2.5 mg. manganous sulphate ($MnSO_4$, $4\,H_2O$) per liter culture solution has a poisoning effect upon *Lemna polyrrhiza,* the growth of which was inhibited. Plants are subject to this toxic effect when the soil in which they grow contains naturally a large amount of manganese or when relatively large amounts of manganous sulphate are supplied artificially — a fact which has been mentioned by several authors (3), (4), (5), (7), (10), (11), (12), (13), (14), (17). The fact that plants cannot help absorbing relatively great amounts of manganese when they grow in markedly acid soil may — besides the high hydrogen ion concentration — be one of the reasons why plants generally will not do well in markedly acid soil, as the toxicity of manganese may here play some rôle. Hitherto aluminium has received particular attention as a growth-inhibitory factor in strongly acid soil, as many authors think that the infavourable influence of the markedly acid soil upon the growth of the plants is due essentially to the concentration of aluminium dissolved in the soil liquid (6), (8), (15), (18), (23)[1]. For aluminium ions are poisonous to plants even when present only in relatively low concentrations.

Several of the cited authors even hold that dissolved aluminium compounds play a greater rôle as a growth-inhibitory factor in markedly acid soil than does the high hydrogen ion concentration; they claim that a high hydrogen ion concentration in the soil is not in itself injurious to the plants, and they base this view on the finding that plants in water culture do very well in acid culture solutions, *e.g.*, Knop's solution with p_H 4.0. This does not hold true in general, however, as there are several plant species which do very poorly in so strongly acid culture solutions. Thus the dry material weight of plants as *Lemna polyrrhiza* (17), *Sinapis alba* (21), *Spinacia oleracea*, and *Beta vulgaris* (see Fig. 1) grown in culture solutions with a p_H value of 4.0 is only 10—15 % of the dry material weight attained by the same plants in culture solutions with a p_H value of 7.0. Indeed the three last-mentioned species are pronounced »lime plants« which cannot thrive on strongly acid soil. On the other hand, plants as *Zea mays*, *Secale cereale* and *Avena sativa* do very well in water culture in solutions with a p_H value of 4.0; but then these species are relatively indifferent also to the hydrogen ion concentration of the soil, and they thrive very well even on rather markedly acid soil if only it contains enough of plant nutrients. Finally, *Hordeum distichum* is the type of a species which behaves somewhat differently, as it cannot thrive on a strongly acid soil but develops very well on water culture in solutions with a p_H value of 4.0, showing no distinct inhibition of growth until the p_H value of the culture solution is lowered to 3.5 (21). In the case of such species it is reasonable to assume, as touched upon above, that their failing ability to thrive on strongly acid soil is not directly due to the high hydrogen ion concentration of the soil but to other growth-inhibitory factors in the soil, *e.g.*, presence of poisonous substances as dissolved compounds of manganese and aluminium. That, in particular, the growth of *Hordeum distichum* is inhibited strongly even by very small amounts of aluminium in solution, while, for example, *Secale cereale* is considerably less sensitive in this respect has been demonstrated by Hartwell and Pember (8), by Ligon and Pierre (15), and by the writer (19).

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[1] Additional references are given by the authors cited here.

It seems probable, therefore, that dissolved aluminium compounds really plays some rôle as a growth-inhibitory factor in strongly acid soil, and this probability is further supported by the findings reported by Gilbert and Pember (6) who in a recent paper have described some water culture experiments which show that different plant species differ in the degree of their sensitiveness to dissolved aluminium compounds. Plants which are not found on strongly acid soil — *e. g., Stellaria media* and species of the genus *Taraxacum* — are very sensitive to aluminium compounds in solution, whereas *Agrostis tenuis,* which is one of the most common plants on acid soil, is far less sensitive to aluminium.

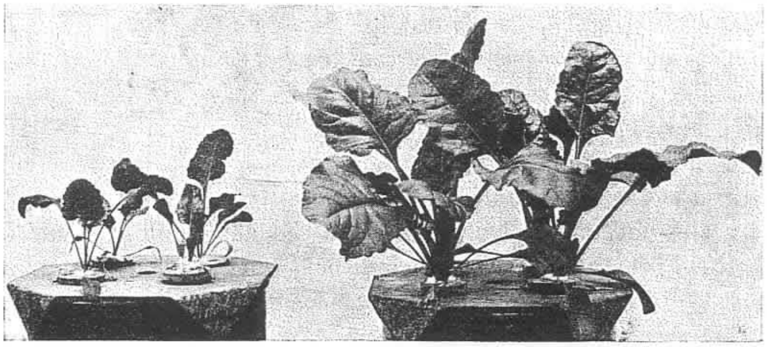

Fig. 1. *Beta vulgaris* (sugar-beet) in water culture in »Knop's solution« of p_H 4.0 and 7.0. When the dry material weight of the plants in the solution of p_H 7.0 is set as equal to 100, the dry material weight of the plants in the solution of p_H 4.0 is equal to 13.

That also manganese compounds in solution may have a growth-inhibitory action in strongly acid soil is evident from the investigations carried out by Jacobsen and Swanbach (10) and by Bortner (3). These authors have shown that tobacco plants in water cultures are relatively sensitive to manganese compounds in solution, as a manganous sulphate concentration corresponding to 15 mg. Mn per liter culture solution exerted strong poisonous effects on the plants. The toxic effects of manganese appeared as definite characteristic symptoms (strong brownish-yellow discoloration of the leaves and partial necrosis of the leaf mesophyl). As exactly the same symptoms appeared when tobacco plants were cultivated on strongly acid soil, and as aluminium poisoning does not produce such symptoms, Bortner concludes that the unfavourable influence of acid soil upon the thriving of tobacco is due to the dissolved manganese compounds contained in the soil.

Plants which normally grow and develop abundantly on strongly acid soil must naturally be able to tolerate the large amounts of manganese which they cannot help absorbing from the soil. On the other hand, it is most likely that plants which thrive only on weakly acid, neutral or basic soil (so-called basic-soil plants or calcicolous plants) cannot absorb so large amounts of manganese as plants indigenous to strongly acid soil without the appearance of strong poisoning effects and resulting inhibition of growth; and this may then be one of the reasons why these plants will not do well on strongly acid soil. As far as the writer knows there has not as yet been published any experiments which were carried out directly from this point of view. Hence the purpose of the water culture experiments to be described in this paper has been to ascertain whether different plants species — in particular, species which differ markedly in their behaviour to the hydrogen ion concentration of the soil — show any difference in sensitiveness to poisoning by addition of increasing amounts of manganous sulphate to the culture solutions.

Water culture experiments with different plant species in culture solutions with addition of increasing amounts of manganous sulphate.

Experimental Plants and Technique. The experiments were made with the following plant species: *Deschampsia flexuosa, Zea mays, Hordeum distichum, Sinapis alba,* and *Senecio silvaticus.*

Among these plant species, the raw humus plant *Deschampsia flexuosa,* is typical of species encountered only on strongly acid soil (19). *Hordeum distichum* and *Sinapis alba* are species which thrive particularly on neutral or faintly alkaline soil, their growth being inhibited markedly with increasing hydrogen ion concentration of the soil, especially as far as *Sinapis* is concerned. *Zea mays* belongs to the species which are relatively indifferent to the hydrogen ion concentration of the soil, thriving nicely on rather strongly acid soil as well as on neutral and weakly alkaline soils (16). Finally, *Senecio silvaticus* is in this respect an intermediate type. It will not do well neither on strongly acid (p_H 4.0) or strongly alkaline (p_H 8.0) soil, whereas it thrives on soil with the p_H value varying within the limits of 5.0—7.0. It is found most frequently and abundantly in woods on soil where the firs have been cut down. In such localities the p_H value of the soil is as a rule between 5.0 and 6.0 (19).

The experiments were carried out in a green-house during the summers of 1934 and 1935. The plants were grown in 5-liter jars, fitted each with a cover with four round holes for four plants. The culture solution here employed was the previously described modification of »Knop's solution« ((20) p. 16 and (21) p. 17), which was prepared with distilled water that had been redistilled in a glass apparatus. Ferric citrate was used as a source of iron in all the experiments (5 mg. Fe per liter).

The manganese content of the culture solutions was varied by adding increasing amounts of a manganous sulphate solution. A constant current of air was pumped through the culture solutions every day for about 4 hours.

Sinapis alba was grown in solutions of p_H 6.0 (this plant cannot be grown in water culture in solutions with a p_H value considerably lower). Two series of culture experiments were made with *Hordeum distichum;* in one series the p_H value of culture solution was 6.0, in the other 4.0. *Senecio silvaticus* was grown in solutions of p_H 5.0, while *Zea mays* and *Deschampsia flexuosa* were grown in solutions of p_H 4.0. The p_H value of the culture solutions was controlled daily and, if necessary, corrected by addition of sulphuric acid or sodium hydroxide, respectively.

The duration of the experiments differed with the different species, according to the rate of growth of each individual species. Thus the experiments with the rapidly growing *Sinapis alba* and *Zea mays* lasted 3—4 weeks, whereas the slow-growing *Deschampsia flexuosa* was grown for a period of two months. In the case of the last-mentioned species, in order to obtain a not all too small plant mass, 6 of the very small seedlings are placed in each cork, making 24 seedlings per culture jar.

At the commencement of the experiment different amounts of manganous sulphate solution were added to the culture solutions so as to give solutions with five different manganous sulphate concentrations, namely: 0.4, 2, 10, 50, and 250 mg. $MnSO_4, 4H_2O$ per liter[1]).

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[1]) In the experiments of 1935 with *Zea mays*, *Deschampsia flexuosa*, and *Hordeum distichum* (the series in which the p_H of the culture solution was 4.0) solutions with 2 mg. $MnSO_4$, 4 H_2O per liter were left out.

At the conclusion of each experiment the plants were weighed, first in fresh condition and later dried (drying at 80° C. to constant weight). In the experiment of 1935 only the weight of the dry plants was determined. Of the dried material only the leaves were used for estimation of the manganese and iron contents. The analytical methods are described previously ((20), p. 5). In several experiments the analysis included also an estimation of the calcium, magnesium and phosphate contents of the leaves (for analytical method, see (21), p. 30).

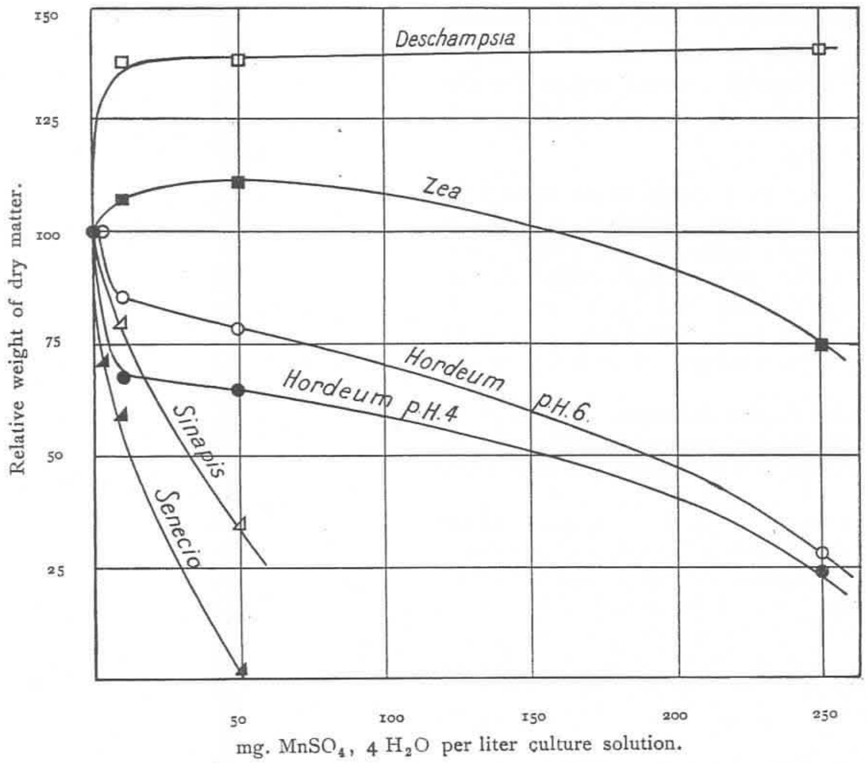

Fig. 2. Water culture experiments with different plant species in culture solutions with addition of increasing amounts of manganous sulphate. The figure shows the relative dry material weight attained by the plants in solutions to which are added increasing amounts of manganous sulphate the dry material weight of the plants grown in the solution containing the lowest manganous sulphate concentration (0.4 mg. per liter) is set as equal to 100).

Toxicity of Manganese to the Different Plant Species. The results of the experiments are given in Table 1 and presented graphically in Figs. 2, 3, 4, 5, 6, and 7. From these it is evident that the different plant species differ very much in their reaction to increasing concentrations of manganous sulphate

Table 1. Water culture experiment with different plant species in culture solutions to which are added increasing amounts of manganous sulphate.

Species	mg. $MnSO_4$, $4\,H_2O$ per liter of culture solution	pH of culture solution	Dry material weight of 4 plants g.	Relative dry mat. weight	% dry mat. in the top	mg. per 100 g. dry leaf material				
						Mn	Fe	Ca	Mg	PO_4
Deschampsia flexuosa	0.4	4.0	0.201	100		6	7.3	251	110	1520
	10.0	4.0	0.276	137		28	6.8	248	106	1700
	50.0	4.0	0.277	138		150	7.4	260	99	1680
	250.0	4.0	0.283	141		368	7.1	283	104	1560
Zea mays	0.4	4.0	10.60	100		10	13.7	691	223	436
	10.0	4.0	11.35	107		28	13.7	658	211	437
	50.0	4.0	11.90	112		110	15.4	682	302	445
	250.0	4.0	7.90	75		330	17.2	652	326	424
Hordeum distichum.	0.4	6.0	6.96	100	10.0	2	8.6	956	193	521
	2.0	6.0	6.93	100	9.9	5	8.8	1030	229	587
	10.0	6.0	6.02	86	10.1	14	7.3	931	211	539
	50.0	6.0	5.42	78	10.9	52	7.3	823	211	532
	250.0	6.0	1.93	28	12.5	164	7.0			
Hordeum distichum.	0.4	4.0	4.22	100		5	10.0			
	10.0	4.0	2.82	67		16	9.0			
	50.0	4.0	2.73	65		55	9.0			
	250.0	4.0	1.02	24		200	—			
Sinapis alba.......	0.4	6.0	5.90	100	9.6	5	10.7	2470	460	1360
	2.0	6.0	5.95	101	9.7	10	16.0	2630	421	1510
	10.0	6.0	4.72	80	10.6	36	15.0	2600	453	1420
	50.0	6.0	2.05	35	10.6	164	15.7			
	250.0	6.0	0.06	1	13.3	—	—			
Senecio silvaticus ..	0.4	5.0	3.34	100	8.7	11	23.0			
	2.0	5.0	2.40	72	8.9	36	19.0			
	10.0	5.0	1.98	59	9.0	63	23.0			
	50.0	5.0	0.07	2	10.0	185				
	250.0	5,0	0.10	3	10.0	457				

in the culture solutions. The raw humus plant, *Deschampsia flexuosa* (Figs. 2 and 3) showed an increasing production of dry material when the manganous sulphate concentration rose from 0.4 to 10 mg. per l. culture solution. The growth was optimal within the concentration limits of 10—250 mg. manganous sulphate per liter, as even the highest manganous sulphate concentration here employed (250 mg. per liter) did not give any inhibition of growth.

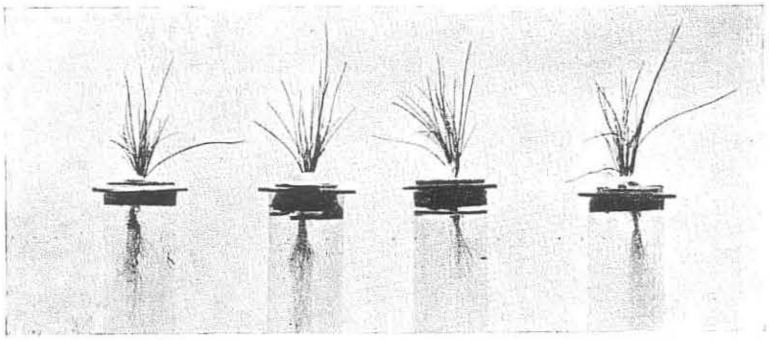

Fig. 3. Plants of *Deschampsia flexuosa* from water culture experiment with addition of increasing amounts of manganous sulphate to the culture solutions. p_H value of culture solutions = 4.0.

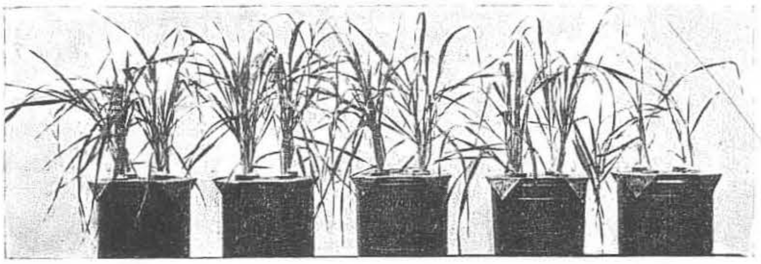

Fig. 4. *Hordeum distichum* in water culture in solutions with increasing manganous sulphate concentration. p_H value of culture solutions = 6.0.

Also the growth of *Zea mays* (Fig. 2) increased, albeit to a less degree, when the manganous sulphate concentration of the culture solution rose from 0.4 to 50 mg. per liter; but the growth was inhibited in the solution containing 250 mg. manganous sulphate pr. liter. The plants that developed in the last-mentioned solution had pale-green leaves which gradually turned greenish-brown in colour.

Hordeum distichum (Figs. 2 and 4), like the next two species, showed optimal growth in the culture solutions with the lowest manganous sulphate concentration (0.4 mg. per liter), and the growth was also optimal in the culture solutions which contained 2 mg. per liter, but then the growth decreased with increasing manganous sulphate concentration. The barley plants which developed in solutions with the highest concentration of manganous sulphate were light greenish-brown in colour.

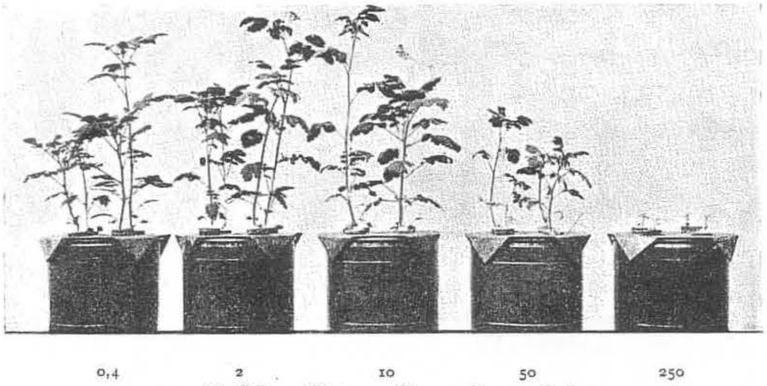

Fig. 5. *Sinapis alba* in water culture in solutions with increasing manganous sulphate concentration. p_H value of culture solutions = 6.0.

From the experiments with *Hordeum distichum*, (Fig. 2) it is evident that the toxicity of manganese asserts itself more strongly in culture solutions of p_H 4.0 than in solutions of p_H 6.0, provided that the manganous sulphate concentration is the same.

Sinapis alba proved to be more sensitive than *Hordeum distichum* to increase in the concentration of manganous sulphate in the culture solution (Fig. 2 and 5)[1]. Thus the solution containing 250 mg. manganous sulphate per liter had a rather rapidly lethal effect on the plants, and with 50 mg. manganous sulphate per liter culture solution the leaves of the plants became gradually brownish-green.

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[1] Here it is to be mentioned, however, that in a culture solution with 10 mg. manganous sulphate per liter the growth of *Hordeum distichum* is inhibited almost just as much as the growth of *Sinapis alba*. In solutions with higher concentrations of manganous sulphate, on the other hand, the growth of *Sinapis* is inhibited far more than that of *Hordeum*.

Among the plant species here examined, *Senecio silvaticus* was found to give the strongest response to increasing concentration of manganous sulphate in the culture solution (Fig. 2 and 6); even a concentration of 50 mg. manganous sulphate per liter was fatal to the plants. This is peculiar insofar as *Senecio silvaticus* is no basic-soil plant, since it grows most frequently on a soil of p_H 5.0—6.0. But it will not thrive on strongly acid soil. A culture experiment with this plant species on strongly acid raw humus soil (p_H 3.8) thus resulted in the development of some small plant individuals which gradually turned yellowish-brown and quite resembled the *Senecio* plants from those water culture experiments in which the manganese poisoning was conspicuously effective. The leaves of these plants contained 137 mg. manganese per 100 g. dry leaf material. Plants of similar appearance are encountered now and then in woods intermediate between raw humus soil and the soil on which *Senecio silvaticus* develops normally. But, as mentioned before, this species is not found on strongly acid soil. As *Senecio silvaticus* grows very well in water culture in strongly acid culture solutions (p_H 3.6—4.0) if only the manganous sulphate concentration is not too high, the reason why this plant will not thrive on strongly acid soil can hardly be the high hydrogen ion concentration of the soil *per se* but must be its relatively large amounts of manganese compounds in solution.

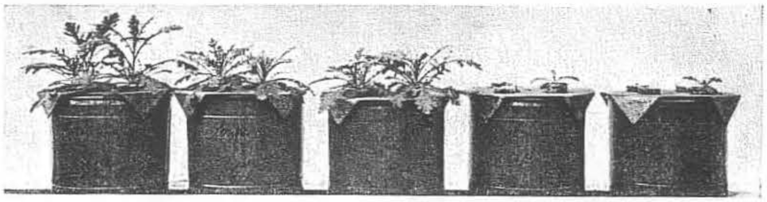

Fig. 6. *Senecio silvaticus* in water culture in solutions with increasing manganous sulphate concentration. p_H value of culture solutions = 5.0.

In the case of *Hordeum distichum*, *Sinapis alba* and *Senecio* *silvaticus* the dry material percentage of the overground parts of the plants was determined too. As shown in Table 1, the dry material percentage of all three plants increases with increasing manganous sulphate concentration of the culture solution.

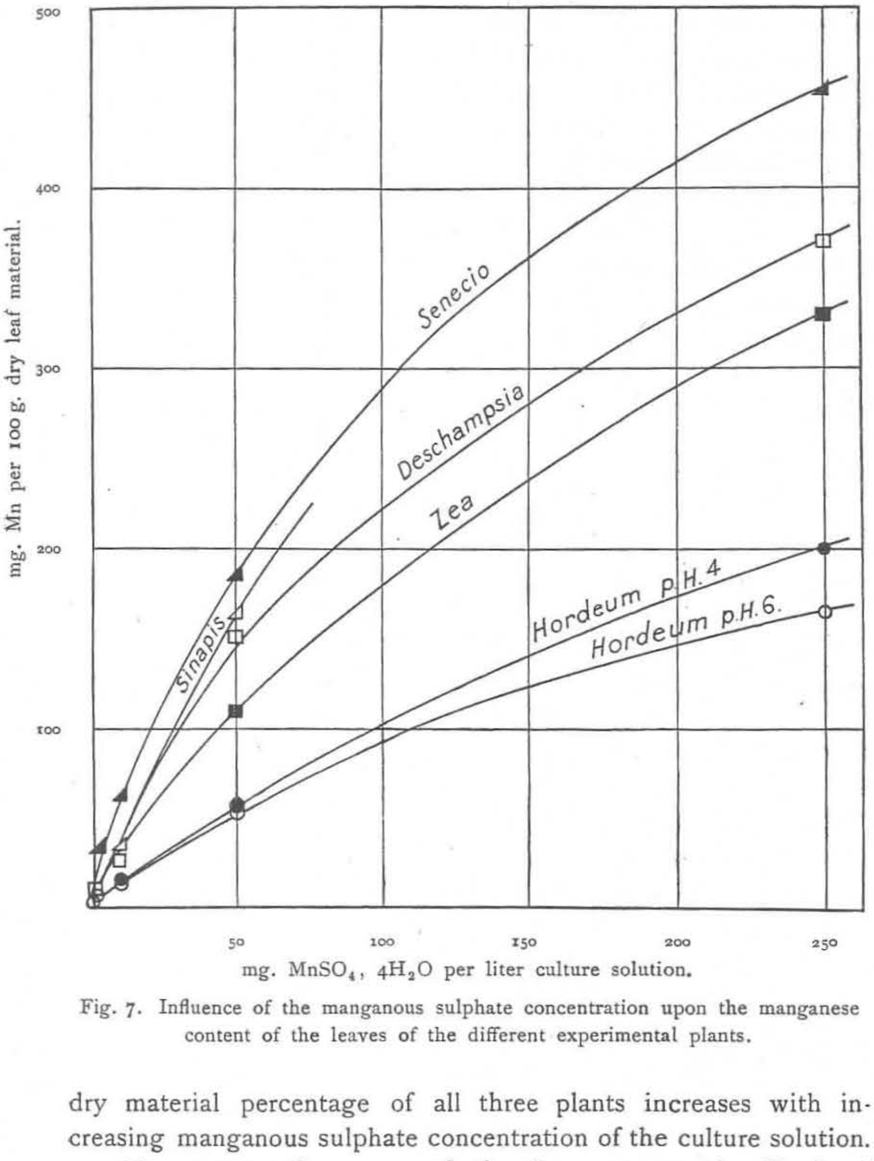

Fig. 7. Influence of the manganous sulphate concentration upon the manganese content of the leaves of the different experimental plants.

Manganese Content of the Leaves at the End of the Experiment. Fig. 7 gives a graphical presentation of the manganese content of the leaves of the different experimental plants with differing concentrations of manganous sulphate in the culture solution (the analytical results are given in Table 1). From these curves it is evident that the amount of manganese absorbed by the plants increases with increasing concentration of manganous sulphate in the culture solution; still, the plants absorb relatively more manganese from solutions with lower concentration of manganous sulphate than from solutions of higher concentration. The curves here depicted take a similar course as the corresponding curves plotted by Hoagland (9) to illustrate the absorption of bromide by *Nitella* from solutions with increasing bromide concentration.

Fig. 7 also shows that the different plant species differ in their capacity for manganese absorption. *Senecio silvaticus* and *Sinapis alba*, which are the most sensitive to increasing concentration of manganous sulphate in the culture solution, show also the greatest manganese absorption. *Hordeum distichum* absorbs considerably smaller amounts of manganese [1]), and this is possibly connected with the fact that this species is less sensitive to increasing concentration of manganous sulphate in the culture solution. In this respect, *Deschampsia flexuosa* and *Zea mays* fall between the other species here employed, absorbing considerably more manganese than *Hordeum*, and less than *Sinapis* and *Senecio*; and evidently they are able to absorb large amounts of manganese without inhibition of their growth.

Iron, Calcium, Magnesium and Phosphate Contents of the Leaves at the End of the Experiment. Besides the manganese content also the iron content of the leaves was determined at the end of the experiment. In addition, also the calcium, magnesium and phosphate contents of the leaves were determined in several instances. The analytical results are given in Table 1 [2]). From these findings it is evident that addition of increasing amounts of manganous sulphate to the culture solution does not bring about any essential changes in the absorption of iron, calcium, magnesium and phosphate by these plants. Rippel (22) claims that a high concentration of manganous sulphate in the culture solution (50—100 mg. per liter) produces chlorosis in oat plants in water culture, as the absorbed manganese is claimed to inhibit or prevent the translocation of iron in the plants — but not the iron absorption from the culture solution. No true chlorosis was observed in my experiments, but the plant species of which the growth was inhibited in solutions with a high concentration of manganous sulphate became pale brownish-green in colour. Want of iron, on the other hand, always manifests itself by a pronounced yellowish-green or yellow colour of the leaves. With absolute absence of iron the leaves may even become almost white.

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[1]) This is in agreement with the previous experiments (20) which showed that *Hordeum distichum* absorbed relatively less manganese from strongly acid soil (p_H 4.2) than did the other experimental plants.

[2]) The calcium, magnesium and phosphate contents of the leaves of *Deschampsia flexuosa* are determined on a dry leaf material from a later water culture experiment with this species performed in exactly the same manner.

Table 1 further shows that the different plant species differ greatly in their capacity for absorption of the same inorganic substance. The same amount of dry leaf material from the acid-soil plant *Deschampsia flexuosa* contains only one-tenth of the amount of calcium which is found in the leaves of the »lime plant« *Sinapis alba* although the calcium concentration of the culture solution was the same in both cases.[1]) Thus *Deschampsia flexuosa* absorbs a relatively very small amount of calcium, and the leaves of the plants that were grown in the culture solution with the highest manganous sulphate concentration contain more manganese than calcium. It is reasonable to assume that an acid-soil plant as *Deschampsia flexuosa* does not tolerate absorption of considerably large amounts of calcium, and that this is a contributory cause of its inability to develop on limy soil as the plant is calcifugous in the true sense of the term. Studies on this question are now being carried out.

On the other hand, *Deschampsia flexuosa* and *Sinapis alba* absorb practically the same amount of phosphate, and their leaves contain about 3—4 times as much phosphate as the leaves of *Zea mays* and *Hordeum distichum*.

SUMMARY

When grown in water cultures, different plant species react very differently to increasing manganous sulphate concentrations in the culture solution.

In the case of *Lemna polyrrhiza* (20) and *Senecio silvaticus* the toxicity of manganese asserts itself even when the culture solution contains only 2 mg. manganous sulphate (= 0.5 mg. man-

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1) It is true that *Deschampsia flexuosa* was grown in a culture solution of p_H 4.0 while *Sinapis alba* was grown in a culture solution of p_H 6.0, but some experiments which are not published yet have shown that the calcium absorption by these two plant species — as well as by several other species — does not change to any particular extent when the p_H value of the culture solution varies within the limits of 4.0—8.0.

ganese) per liter. A culture solution containing 50 mg. manganous sulphate per liter is lethal to these plants.

In the case of *Hordeum distichum* and *Sinapis alba* no toxic effect was observed until the culture solution contained 10 mg. manganous sulphate (= 2.5 mg. manganese) per liter. A culture solution containing 250 mg. manganous sulphate per liter was lethal to *Sinapis alba* plants and strongly inhibitory to the growth of *Hordeum distichum*. In experiments with *Hordeum distichum* manganese was found to have a stronger toxic effect in culture solutions of p_H 4.0 then in culture solutions of p_H 6.0.

The growth of *Zea mays* is promoted when the manganous sulphate concentration of the culture solution increases from 0.4 mg. to 50 mg. per liter, and the growth of this species is not inhibited till the culture solution contains 250 mg. manganous sulphate per liter.

Deschampsia flexuosa attains its optimal growth in culture solutions with a manganous sulphate concentration within the limits of 10—250 mg. per liter. It grows less abundantly in a culture solution containing 0.4 mg. manganous sulphate per liter.

So *Deschampsia flexuosa* which thrives very well on strongly acid soil is able to tolerate far higher concentrations of manganous sulphate in the culture solution than are species as *Hordeum distichum*, *Sinapis alba* and *Senecio silvaticus*, which will not do well on strongly acid soil. Thus the experiments indicate that the amount of dissolved manganese compounds in the strongly acid soil plays an essential rôle as a growth-inhibitory factor. The fact, that only a small number of plant species (acid-soil plants) can thrive on strongly acid soil is due not only to the high hydrogen ion concentration of the strongly acid soil *per se*, but also to the circumstance that manganese is so poisonous to most plant species that they cannot tolerate the amounts of manganese they have to absorb from the strongly acid soil. Several authors have demonstrated that also the poisonous effect from dissolved aluminium compounds plays a rôle as a growth-inhibitory factor in strongly acid soil.

The lowest concentrations at which the toxicity of manganese asserts itself are of the same magnitude as the lowest concentrations at which the poisoning effect of aluminium may be demonstrated. In the case of *Lemna polyrrhiza* and *Senecio silvaticus*, as mentioned above, inhibition of growth appeared already in culture solutions containing 0.5 mg. manganese per liter; in the case of *Sinapis alba* and *Hordeum distichum*, however, this effect was not noticeable until the culture solution contained 2.5 mg. manganese per liter. According to *Ligon* and *Pierre* (15), the lowest concentration at which the toxicity of aluminium has been demonstrated is 1 mg. aluminium per liter culture solution.

Possibly the calcium ion concentration of the culture solution modifies the toxic effect of manganese on the plants as it has been demonstrated that calcium ions in their action are antagonistic to manganous ions (1), (2). But this question has not been studied in compound culture solutions. If the poisonous effects of manganese increase with decreasing calcium ion concentration of the culture solution, it means that manganese will have an even more toxic action in strongly acid soil than would be expected after the water culture experiments here described, for the calcium ion concentration of strongly acid soil is exceedingly low.

As the manganous sulphate concentration of the culture solution is increased, the plants absorb increasing amounts of manganese; yet, they absorb relatively more manganese from solutions with lower concentrations of manganous sulphate than from solutions with higher concentrations of this salt. The different plant species differ very much in their absorption of manganese from culture solutions with the same manganous sulphate concentration.

In conclusion I wish to express my thanks to the director of the laboratory, Professor S. P. L. Sörensen for the never failing interest with which he has followed this work.

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